

THE REPRODUCTIVE BIOLOGY AND HOST SPECIFICITY OF  
*OROBANCHE PINORUM* GEYER (OROBANCHACEAE)

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ABSTRACT

This study is the first examination of the reproductive biology of *Orobanche pinorum* Hook., a rare, parasitic flowering plant of western North America. Plants from six separate populations were treated to test reproductive strategies, including xenogamy, autogamy, and agamospermy. Seeds that developed from the flowers of treated plants were counted to determine the reproductive success of each strategy. The results showed *O. pinorum* to be predominantly autogamous, producing a mean of nearly 700 seeds per capsule and over 70,000 seeds per plant. There was some evidence for xenogamy, but potential pollinators were seen only on six occasions in three years. Two were collected—solitary bees *Osmia exigua* and *Ashmeadiella cactorum*. No evidence was found for agamospermy. *Orobanche pinorum* appeared to parasitize only one host—the shrub *Holodiscus discolor* (Pursh) Maxim.

INTRODUCTION

*Orobanche pinorum* Hook. (pine broomrape, Fig. 1a–d) is in the Orobanchaceae, a family of achlorophyllous, obligate root parasites (Kuijt 1969). An endemic of western North America, this uncommon species has been found from northern California through Oregon, and north to central Washington and Idaho (Munz 1930; Hitchcock et al. 1959; Abrams and Ferris 1960; Heckard 1993). In Washington state, *O. pinorum* is listed as a “monitor” species due to its relative rarity (Washington Natural Heritage Program 1997). A literature search provided no published studies on this species other than descriptive reports and a single chromosomal count in one specimen (Heckard and Chuang 1975).

The flowers of Orobanchaceae are apparently adapted for cross-pollination, displaying traits typically associated with bee pollination—tubular corolla complete with landing platform, nectar guides, contrasting colors around the floral entry, and nectar rewards (Kuijt 1969). The campanulate corolla of the zygomorphic flowers is yellowish with purple exterior veins which probably serve as nectar guides. The two broad, deltoid lobes of the upper lip form a hood over the stamens and stigma while the three lanceolate lobes of the lower lip provide a potential insect landing platform (Fig. 1a–c).

Reproductive strategies besides xenogamy have

also evolved within Orobanchaceae. While the flowers of most species are chasmogamous, cleistogamy has been reported in *Epifagus*, *Cistanche*, and *Boschniakia* (Thieret 1971; Musselman 1980; Olsen and Olsen 1980). Although Kuijt (1969) argues that insects play the most important role in pollination, the work of Musselman (1980) and Musselman et al. (1981) show autogamy to be commonly employed in varying degrees. Jenson (1951) found that populations of *Orobanche uniflora* L. in New England were obligately agamospermous, and Reuter (1986) found that populations of *Orobanche fasciculata* Nutt. in Wisconsin produced similar numbers of seeds via agamospermy, autogamy, and xenogamy.

Species within Orobanchaceae parasitize a variety of herbaceous and woody host species (Musselman 1980). The majority of broomrapes appear to have broad host ranges, with more narrow host-specificity found occasionally among physiological races (Musselman 1980). Although most references suggest *O. pinorum* is hosted by coniferous species (Geyer 1851; Hitchcock et al. 1959; Munz and Keck 1968; Peck 1961), the most recent accounts (Heckard 1993; Smith-Kuebel and Lillybridge 1993) suggest instead the shrub *Holodiscus discolor* (Pursh) Maxim.

The purpose of this study was to examine the reproductive strategy of *O. pinorum*, collect and identify any potential pollinators, and examine host specificity.

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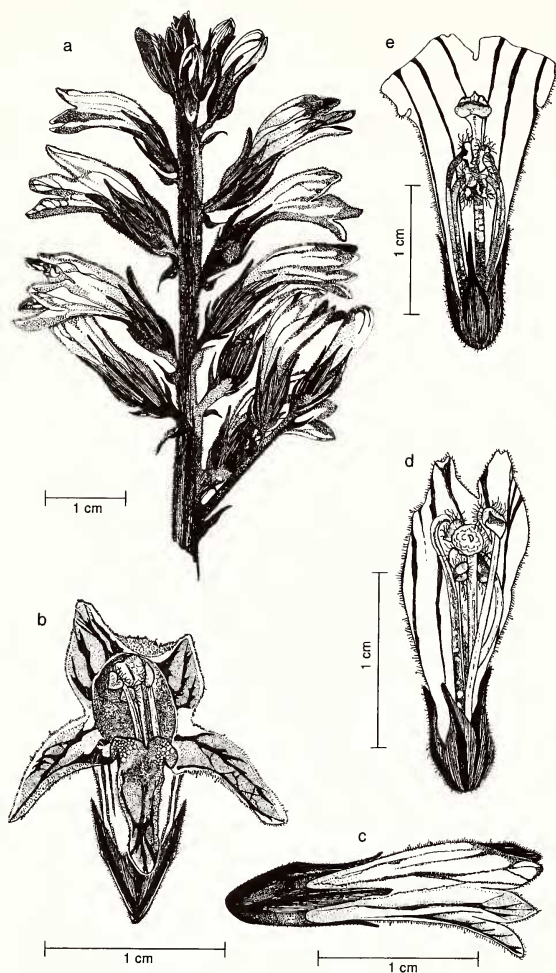


FIG. 1. a. upper  $\frac{1}{3}$  of *Orobancha pinorum* stalk with flowers and terminal buds. b. frontal view of *O. pinorum* flower. c. lateral view of *O. pinorum* flower. d. *O. pinorum* flower with ventral half of corolla tube excised. e. *O. uniflora* flower with ventral half of corolla excised. Drawings by Eve Ponder.

## METHODS

**Study area.** All field research sites were located in Washington state, within the Leavenworth Ranger District of the Wenatchee National Forest. The

sites were on moderate to steep slopes, in lithosolic substrates with gravitational instability and poor horizontal development. The forest communities were generally mixed-coniferous, dominated by *Pseudotsuga menziesii* (Mirbel) Franco, *Pinus ponderosa* Laws., and *Abies grandis* (Douglas) Lindley with less than 50% canopy cover. The area is underlain by the Chumstick Formation, a bedrock composed of middle Eocene materials including micaceous feldspathic sandstone, interbedded pebbly sandstone, conglomerate, and shale (Tabor et al. 1987). The great soil groups in this region include cryorthods, haplorthods, and xerochrepts (Franklin and Dyrness 1973). The climate is characterized by warm to hot summers (maximum temperatures approaching 38°C) and cold winters (minimum temperatures below -18°C) (Donaldson and Ruscha 1975). Mean annual precipitation at the study sites ranges from 64–89 cm with two thirds falling between October and March. The summers are characterized by drought, with less than 2.5 cm of rain falling from July through August. Table 1 provides summary descriptions of the study sites.

Individuals of *O. pinorum* from six populations were selected and treated in two reproductive experiments. Data from two additional populations were used to estimate the mean number of flowers per plant. In this study, populations of *O. pinorum* were considered distinct if they were separated by at least a half mile with no individuals found between populations. Data were collected during the growing seasons of 1993, 1994, and 1995.

**First reproduction experiment.** Six treatments were applied to test reproductive strategies of *O. pinorum* (Table 2). The criteria for selecting plants were health and phenology. In each population, plants were selected if they appeared healthy and showed no visible signs of insect infestation (i.e., caterpillar silk, feces, or herbivory). To ensure that all reproductive structures would be well developed, buds just prior to anthesis were treated. Treatments were assigned randomly to each suitable plant, using a calculator's random function. For each treatment, eight plants from five different populations (Sites 1–5) were selected with two flower buds treated per plant.

In Treatment 1 (T1), autogamous seed production

TABLE 1. APPROXIMATE LOCATION, ASPECT, POPULATION SIZE, SLOPE AND ELEVATION OF *O. PINORUM* STUDY SITES. All sites were located in Washington state, within the Leavenworth Ranger District of the Wenatchee National Forest.

Site #	Elev. (m)	Slope (°)	Aspect	Pop. size	Location
1	720–1100	30–45	w	>100	Negro Creek
2	880	20–30	e	16–34	North Ruby Creek
3	830	30	e	2–5	South Ruby Creek
4	610	10	sw	3–9	Lower Camas
5	990	<10	e	9–22	Upper Camas
6	1170	30	se	2–3	King Creek
7	520–670	40	n	>100	W. Spromberg Canyon
8	500–575	40	n	41	E. Spromberg Canyon

TABLE 2. TREATMENT DESCRIPTIONS FOR THE FIRST REPRODUCTION EXPERIMENT.

Treatment #	Treatment test	Treatment procedure
T1	Autogamy	Flowers bagged to exclude pollinators
T2	Control	Flowers not bagged or modified
T3	Potential Xenogamy	Flowers emasculated and hand-crossed
T4	Vectoral Xenogamy	Flowers emasculated, open to pollination
T5	Agamospermy-1	Flowers emasculated, bagged to exclude pollinators
T6	Agamospermy-2	Flowers emasculated, stigmas excised, bagged to exclude pollinators

was tested by bagging the selected buds in a tight-weave cotton cloth to exclude pollinators and wind-borne pollen. In T2 (Control), selected plants and buds were left unmodified. In T3 (Potential Xenogamy), buds selected were emasculated and hand-crossed with pollen from other plants to test the potential for seed production via vectoral cross-pollination (insects, wind, etc.). In T4 (Vectoral Xenogamy), buds selected were emasculated and left open to pollination to test directly for xenogamous seed production. In T5 (Agamospermy-1), buds selected were emasculated and then bagged to exclude pollinators and wind-borne pollen to test for agamospermy. In T6 (Agamospermy-2), both anthers and stigmas were excised from the selected buds, and the buds were then bagged to exclude pollinators and wind-borne pollen. This treatment provided a more thorough test of agamospermy, since no stigmatic surface was available for the germination of pollen that the experimental design might fail to exclude from the flower.

Once the capsules of the treated buds matured, they were collected prior to dehiscence and stored to dry. Once dry, the capsules were opened and the seeds removed and spread evenly on a grid and counted under 15 $\times$  magnification.

*Second reproduction experiment.* Four treatments were applied to test for the relative success of four potential pollination strategies in *O. pinorum* (Table 3). Again, healthy and phenologically suitable plants were selected for treatment, and the treatments were applied randomly for each plant, using a calculator's random function. Nine plants were selected for each treatment from sites 1–6. As in the first pollination experiment, flower buds that appeared ready to open were selected for treatment. For each treatment, the entire plant was bagged to exclude potential pollinators and wind-borne pol-

len. Capsules were collected and seeds removed and counted as in the first reproductive experiment.

In T1 (Xenogamy/Vicinism), selected buds were emasculated and hand-crossed with pollen from flowers on nearby plants in the same population to test the potential reproductive success of vicinism. In T2 (Xenogamy/Non-Vicinism), buds selected were emasculated and hand-crossed with pollen from different populations to test the potential reproductive success of xenogamy between plants less likely to be related. All cross-pollinations in T2 were made between plants from populations separated by at least one mile. In T3 (Potential Geitonogamy), buds selected were emasculated and hand-pollinated with pollen from flowers on the same plant to test the potential reproductive success of geitonogamy. In T4 (Geitonogamy), buds from the middle or lower portions of the plant were emasculated and left available for pollination via pollen falling from flowers above them.

Although the bag would help prevent wind from blowing pollen from one flower to another, pollen that did exit a flower might fall onto flowers below. For that reason, buds tested in treatments T1–T3 were all located at the tops of plants so that no flowers were directly above them.

Unlike the first reproduction experiment, hand-crossing was employed as the pollination method in the treatments T1–T3. In this way, potential variations in results due to the different success rates between hand-pollination and natural self-pollination were averted.

*Statistics.* The research was designed for the two reproductive experiments so that all data could be analyzed by Analysis of Variance (ANOVA) using a completely randomized design with subsampling. The alpha level of significance was preset at 0.05.

The mean number of seeds per capsule for *O.*

TABLE 3. TREATMENT DESCRIPTIONS FOR THE SECOND REPRODUCTION EXPERIMENT. All plants bagged to exclude pollinators. All flowers emasculated.

Treatment #	Treatment test	Treatment procedure
T1	Xenogamy/Vicinism	Flowers hand-crossed with pollen from plants in the same population
T2	Xenogamy/Non-Vicinism	Flowers hand-crossed with pollen from plants in different populations
T3	Potential Geitonogamy	Flowers hand-crossed with pollen from other flowers on the same plant
T4	Geitonogamy	Flowers selected from the middle or lower region of the inflorescence



TABLE 4. MEAN SEED COUNTS PER CAPSULE FOR THE FIRST REPRODUCTION EXPERIMENT. \* Treatments significantly different at the 0.05 level.

Mean	Treatment						Treatment test	
	#	T1	T2	T3	T4	T5		T6
868	T1		*	*	*	*	*	Autogamy
689	T2	*		*	*	*	*	Control (unmodified)
248	T3	*	*		*	*	*	Potential Xenogamy
13	T4	*	*	*				Vectoral Pollination
0	T5	*	*	*				Agamospermy-1 (emasculated only)
0	T6	*	*	*				Agamospermy-2 (emasculated and stigma excised)

*pinorum* was calculated from the data in T2 (Control) of the first reproduction experiment. The mean number of flowers per plant was calculated from 33 plants over a two-year period. An estimated mean number of seeds per plant was then derived by multiplying the mean number of flowers per plant by the number of seeds per capsule.

*Potential pollinators.* Over 100 hours were spent observing plants for insect pollination activities. These observations were made during visits to the sites for data collection, applications of experimental treatments, and fruit collections. Since preliminary observations suggested that there were few if any insect pollinators, no systematic method of observation was employed. The importance of flower visitors was inferred by a combination of factors: the number of observed visitations, pollen load ratios, insect behavior, and the results of treatments that tested for xenogamy. Pollen load ratios of insect specimens were determined using a dissecting microscope and pollen was identified by comparing the grains with those taken from *O. pinorum* anthers.

*Host specificity.* Four specimens of *O. pinorum* were excavated (including one in Oregon) to identify the host species. Host roots were located and traced back to their sources. Since *O. pinorum* is rare in Washington, Oregon, and California (Jepson 1970; Heckard 1973; Heckard and Chuang 1975; Heckard 1993), the number of excavations were intentionally limited in number.

## RESULTS

*First reproduction experiment.* The mean numbers of seeds per capsule for each of the six treat-

ments are given in Table 4. The treatment testing for autogamy showed the highest production of seeds, with the control a close second. The hand-crossed treatment testing for potential Xenogamy produced less than half as many seeds as the control and autogamy treatments, but nearly 20 times more than the test for naturally occurring vectoral pollination. Neither treatment for agamospermy produced any seeds at all.

*Second reproduction experiment.* The mean numbers of seeds per capsule for the four treatments are given in Table 5. The capsules in Treatments T1 (Xenogamy/Vicinism), T2 (Xenogamy/Non-Vicinism), and T3 (Potential Geitonogamy) did not produce significantly different numbers of seeds from each other, but produced significantly more seeds than capsules in T4 (Geitonogamy).

*Seed production.* The mean number of flowers per plant was 96 (95% Confidence Interval {CI}  $\pm$  14) and the mean number of seeds per capsule was 689 (95% CI  $\pm$  126). The estimated mean number of seeds per plant is 71,656.

*Potential pollinators.* During the summers of 1993, 1994, and 1995, insects were seen entering *O. pinorum* flowers on only six different occasions. All were small hymenopterans. Two were collected and identified as solitary leafcutting bees in the superfamily Apoidea, family Megachilidae (Dr. Terry Griswold, bee taxonomist, Utah State University, Logan, UT, personal communication). *Ashmeadiella cactorum* is a small, long-tongued, dark brown bee with light stripes derived from densely packed white hairs at the sulci separating the abdominal tergites. The second species was *Osmia exigua*, a slightly larger, long-tongued green bee. Just before capture, both bees had been actively and systematically entering flowers, crawling completely into the corolla tube, then backing out, flying to another flower, and repeating the process. *Osmia exigua* could be heard apparently buzz-pollinating the flowers it entered, suggesting that it was actively collecting pollen.

Both bees had a ventrally located abdominal scoop where the majority of pollen grains were collected. Pollen examined on the body of *A. cactorum* was exclusively that of *O. pinorum*. The body of *O. exigua* held two types of pollen, approximately

TABLE 5. MEAN SEED COUNTS FOR THE SECOND REPRODUCTION EXPERIMENT. \* Treatments significantly different at the 0.05 level.

Mean	Treatment				Treatment test
	#	T1	T2	T3	
319	T1			*	Xenogamy/Vicinism
264	T2			*	Xenogamy/Non-Vicinism
194	T3			*	Potential Geitonogamy
16	T4	*	*	*	Geitonogamy

75% of which was from *O. pinorum* (the other pollen type was not identified).

*Host specificity.* In all four excavations of *O. pinorum*, the host root was traced back to *H. discolor*. Although species composition varied at *O. pinorum* sites, all *O. pinorum* individuals seen in this study were found within five meters of one or more *H. discolor* plants.

#### DISCUSSION

*Reproductive strategy.* The results suggest predominant autogamy is the reproductive method employed by *O. pinorum* (although pseudogamy has not been ruled out). Facultative autogamy is a common reproductive strategy for annuals and parasites, and for species within Orobanchaceae in particular (Holzner 1982; Musselman et al. 1981). Open habitats select for colonizing species, and successful colonizers tend to have restricted recombination systems (Grant 1981; Begon and Mortimer 1986). Such colonizers can rapidly multiply and occupy a site.

Although the flowers of *O. pinorum* show most of the hallmarks of bee pollination, the positioning of their stamens promotes selfing. In *O. uniflora*, the predictable arrangement of the androecium relative to the stigma would tend to discourage self-pollination and facilitate crossing (Fig. 1e). The short filaments prevent the anthers from reaching the stigma, and the anthers are located beneath the more or less horizontal style. In this way the stigma is positioned to receive pollen carried from other flowers by the intruding insect pollinator. As the vector continues further, the anthers are positioned to dust it with pollen. In contrast, the maturing anthers of *O. pinorum* flowers examined in this study grew toward the stigma, with one or more contacting it directly (Fig. 1b, d). Hairs on the pollen sacs became entangled in the sticky fluid of the stigmatic surface, so that when the anthers dehisced, self-pollination was assured. As a result, the majority of ovules were self-fertilized, producing hundreds of seeds per capsule without relying on the vagaries of insect vectors. In this study, insect pollination accounted for an average of less than 20 mature seeds per capsule while self-pollination produced an average of nearly 700 (Table 4).

The parasitic habit of this species is highly specialized, and *O. pinorum* appears to occupy a niche with few if any direct competitors. One may predict that inbreeding would tend to maintain genetic stability in this parasite, and that predominant autogamy would in turn be reinforced by the stabilizing selection of its parasitic niche (Grant 1981). Thus predominant autogamy provides a stabilizing mechanism for this parasite as well as a means of dependably high seed production necessary to assure continued contacts with its host.

No evidence was found for pollen selection other than first-come-first-served, since pollen from the

same plants, neighboring plants, and plants in distant populations all produced seeds with equal success. The apparently homogamous flowers of *O. pinorum* ensure selfing, which occurs approximately at (and on rare occasion before) the onset of anthesis. With no physiological barrier to xenogamy, *O. pinorum* retains the potential for cross-pollination and the subsequent infusion of new genetic variation.

*Apparent pollinators.* The recovery of two flower-visiting hymenopterans lends support to the potential for occasional out-crossing. That the pollen loads of both bees were composed primarily of *O. pinorum* pollen (entirely on *A. cactorum*) suggests a specificity that could be the result of a long-term relationship between pollinator and plant. Although the average vectoral seed production shown in this study was very low (13/flower, Table 4), its occurrence establishes out-crossing as a clear possibility.

Still, the evolutionary direction may be toward increasingly restricted recombination. The findings here document that insect visitation is infrequent and likely to be preceded by self-pollination when it occurs. Furthermore, many if not most visits by hymenopteran vectors may result in geitonogamous pollination, as they systematically probe successive flowers on the same plant.

The occasional dehiscence of *O. pinorum* anthers before anthesis noted in this study suggests the possibility of a trend toward cleistogamy. Olsen and Olsen (1980) found that a population of *Boschniakia hookeri* Walp., a related species within Orobanchaceae, had achieved obligate autogamy via cleistogamy.

*Host specificity.* The type specimen of *O. pinorum* was collected by Andreas Geyer nearly 150 years ago (Geyer 1851). In his notes he wrote that it was "growing on the roots of *Abies balsamea*." It seems evident that Geyer coined the epithet *pinorum* based on what he assumed was the host family. Most of the regional floras and identification books that followed mention coniferous hosts for *O. pinorum* (Munz 1930; Hitchcock et al. 1959; Abrams and Ferris 1960; Munz and Keck 1968; Peck 1961), but most fail to mention the host species, and the reliability of these accounts is doubtful. Musselman (1980) questioned the biological veracity of many reported hosts of species in Orobanchaceae. There appears to be no mention in the literature of gymnosperm hosts for any of the Orobanchaceae other than *O. pinorum*. Confirmation of such a finding would be an important contribution.

Abrams and Ferris (1960) mention anecdotal reports of *O. pinorum* parasitizing *H. discolor*, which may be the earliest published suggestion of this association. Major and Taylor (1977) list "*Holodiscus microphyllus* (with *Orobanche pinorum*)" among alpine vegetation habitats in California's Cascades. Two recent works also name *Holodiscus* as the host. Heckard (1993) mentions "*Holodiscus* spp."



which suggests the possibility that *H. discolor*, *H. microphyllus*, and *H. boursiéri* might all be hosts. He goes on to state emphatically that *O. pinorum* is "not known on conifers." Finally, Smith-Kuebel and Lillybridge (1993) specifically mention *H. discolor* as the host, and include the comment that *O. pinorum* was "originally thought to be parasitic on conifers." The findings of this study on host specificity, although limited, support these last two reports.

A species limited to a single host appears unusual in Orobanchaceae. The range of host families is very diverse, including herbs, shrubs, and trees. Monocot hosts are rare, and gymnosperm hosts may not exist. Musselman (1980) argues that most species in Orobanchaceae are very promiscuous, with broad host ranges, and that only physiological races are restricted to narrow host ranges. Furthermore, he claims that *O. crenata* may have the most narrow host range, restricted to legumes. Thus *O. pinorum* may be unusual in having a narrow host range—possibly the most narrow within Orobanchaceae—if it is truly restricted to three or fewer *Holodiscus* species.

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